



COMPUTER MODELING OF THE BIOTIC CYCLE FORMATION IN A CLOSED ECOLOGICAL SYSTEM

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ABSTRACT

The process of biotic turnover in a closed ecological system (CES) with an external energy flow was analyzed by mathematical modeling of the biotic cycle formation. The formation of hierarchical structure in model CESs is governed by energy criteria. Energy flow through the ecosystem increases when a predator is introduced into a “producer-reducer” system at steady state. Analysis of the model shows that under certain conditions the presence of the primary predator with its high mineralization ability accelerates the biotic turnover measured by primary production. We, therefore, conclude that for every system it is possible to find a suitable predator able to provide the system with a higher biotic turnover rate and energy consumption.

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INTRODUCTION

A lot of efforts have failed to find precise formal connections and derive energetic principles of the evolution of life. A direct application of the laws of thermodynamics to the analysis of life phenomenon has led to a contradiction: the evolution (development) of living systems occurs in the opposite direction predicted by the second law of thermodynamics. Instead of degradation of the system and an increase of entropy, in living systems we observe an enhancing of system structure. A thermodynamic criteria of the evolution of open systems is derived in nonequilibrium thermodynamics. In application to living systems, whose openness to the flow of energy is the most important property, such criteria determine stability of the steady state where the rate of the entropy production (and a dissipation of the energy) is minimal (Nicolis & Prigogine, 1977). The physical criteria of evolution do not correspond to this theoretical situation since living systems have definitely increased their use of free energy and the dissipation of energy as well (Odum, 1971; Morowitz, 1968; Pechurkin, 1982).

Species evolution has become a dominant theory in contemporary biology following the impact of Darwin's ideas on natural selection. However, from the position of a holistic approach the limitations of such a viewpoint are obvious. For a given species natural selection acts in a stochastic, undetermined manner; therefore, in the framework of a species-based approach it is impossible to find general criteria accounting for living system development.

Holistic viewpoints on the integration of the world of living organisms and their environments and the tight relationship between the development of living organisms and their powerful impact on the Earth's environment were recognized more later (Vernadsky, 1926; see recent references in Pechurkin, 1994; Gitelson, 1999). In ecological systems it is very difficult to measure entropy whereas a change in free energy of the system relative to its environment can be assessed very precisely. The analogous term, exergy, decreases with the dissipation of free energy, and increases with its acquisition, and with increased exergy there is also increase in complexity (Jorgensen et al., 1992; Jorgensen, 1997). Our

understanding of natural selection changes its role following this approach: from the role of a God determining the evolution of individual species, to an important vector in the progressive development of biotic cycles (Darwin-Vernadsky approach). The action of natural selection is controlled not only on the level of species formation, but at the level of development of whole ecosystem cycles.

It seems reasonable that if one takes the ecosystem (with its biotic cycle as its base) as an evolutionary unit then all chains of the ecosystem must evolve connectedly. Therefore, in each biotic chain only certain species would survive. Such a species would better manage the energy flow through its population which would lead to an increase of free energy flow obtained by the first chains in the ecosystem (evaluated as primary production). With mathematical modeling of the formation and development of biotic cycles we shall investigate the validity of such a viewpoint.

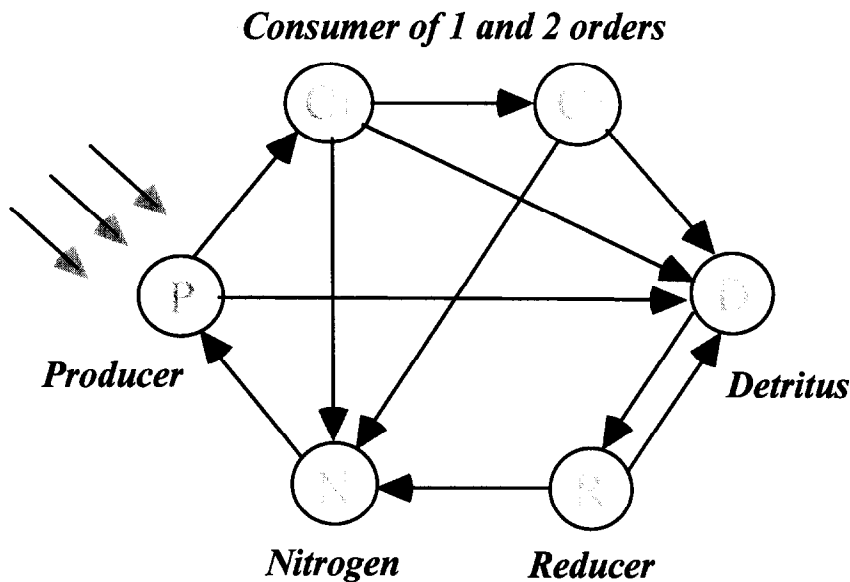


Fig. 1. A diagram of the biotic cycle in a simple model ecosystem.

MATHEMATICAL MODEL

A diagram of the biotic cycle limited by nutrients in a small laboratory water microecosystem is shown on Figs. 1, 2 (see for details, Bril'kov et al., 1994). Basic ecosystem chains are represented by producers *P* (autotrophs, green singlecellular algae such as *Scenedesmus*, *Clorella sp.*), consumers of first (*C*₁, *Daphnia pulex*) and second order (*C*₂, fishes guppy *Lebistes reticulata*), detritus (*D*), reducers (*R*, microorganisms) and the concentration of essential life nutrients (e. g. nitrogen, *N*). For the growth of producers, light energy is also required. It is assumed that the growth of producers is limited by the concentration of available nutrients (nitrogen). Therefore, there is no excretion of nitrogen as a metabolite. In contrast, the growth of consumers (first and second order) is limited by the energetic resources contained in their prey. Energy flow into the model ecosystem was measured as primary production (production of green algae, Fig. 3). Free nitrogen is excreted immediately in the medium after prey consumption. Detritus (non- living organic material) is produced after death of all components of the

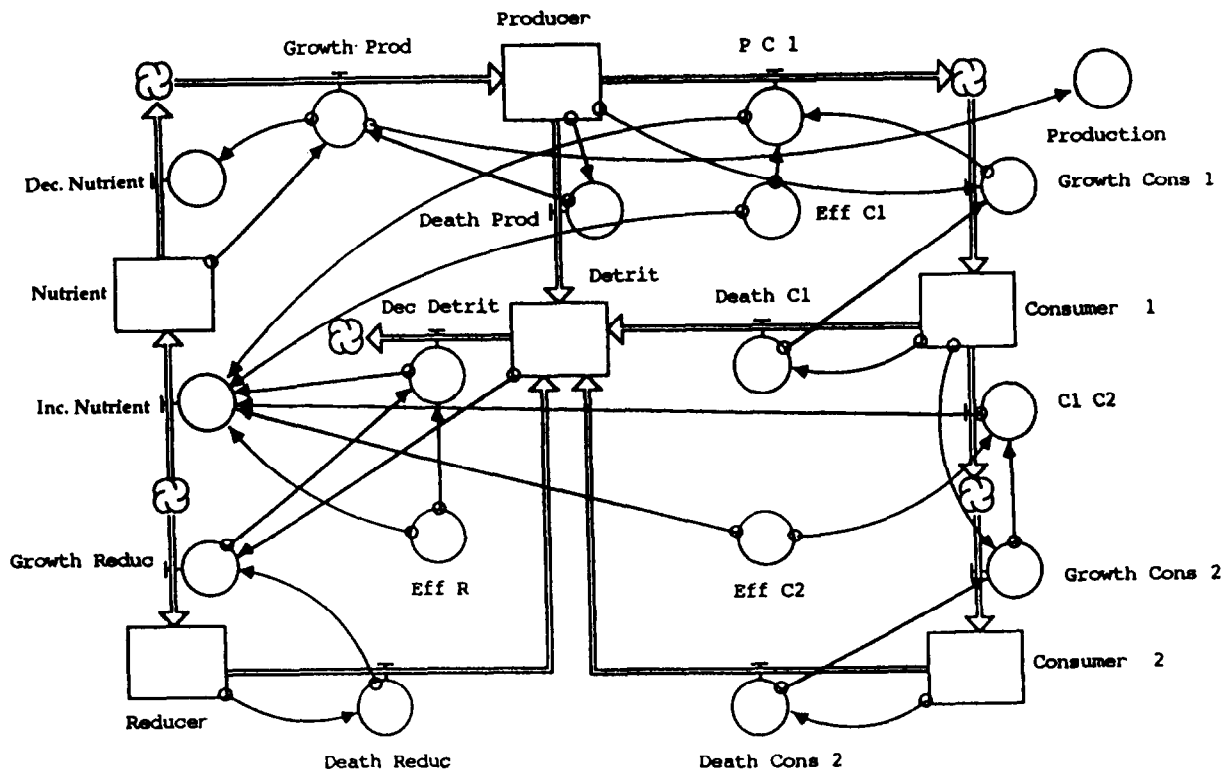


Fig. 2. Stella-II diagram of the biotic cycle in a simple model ecosystem (fig. 1).

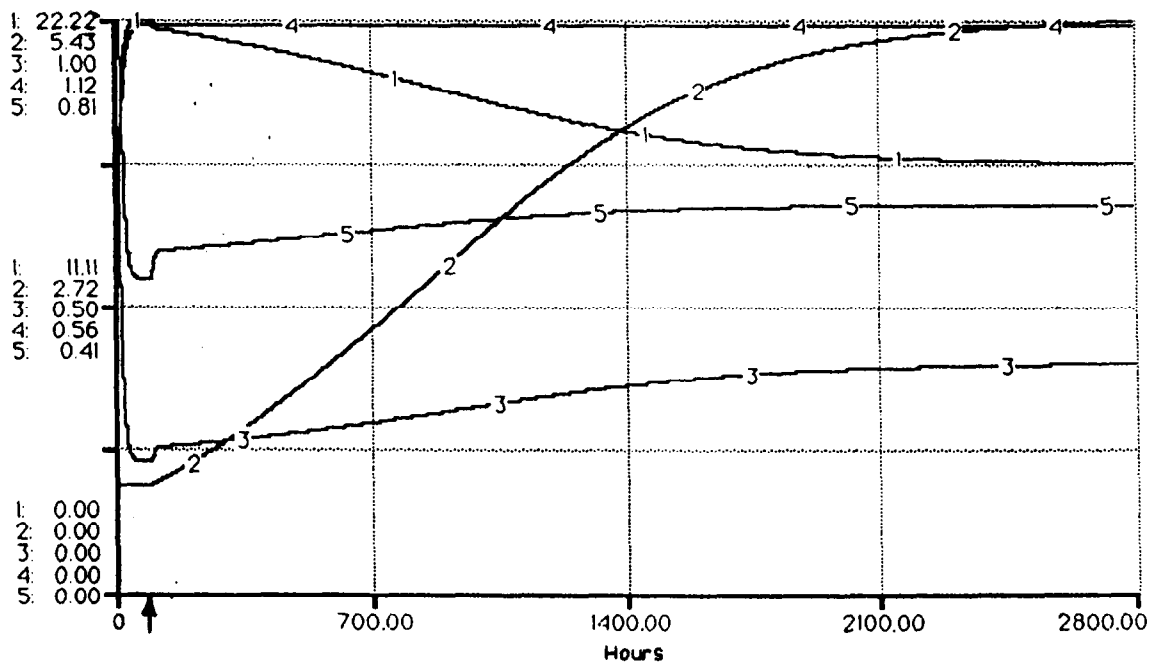


Fig. 3. Increase of energy flow in the model ecosystem, measured as primary production, after introduction of consumers of 1st and 2nd order to simple ecosystem consisting of producer, detritus-reducer, and nutrients.

Curves (1-4 mg/l): 1 - producer, 2 - consumer, 3 - nutrients, 4 - detritus, 5 - primary production ($\text{mg l}^{-1}\text{h}^{-1}$). Pointer - a moment of introduction of consumer.

$$\begin{aligned}
\frac{dP}{dt} &= \mu_p P - \varepsilon_p P - \frac{\mu_{C_1} C_1}{Y_{C_1}} \\
\frac{dC_1}{dt} &= \mu_{C_1} C_1 - \varepsilon_{C_1} C_1 - \frac{\mu_{C_2} C_2}{Y_{C_2}} \\
\frac{dC_2}{dt} &= \mu_{C_2} C_2 - \varepsilon_{C_2} C_2 \\
\frac{dD}{dt} &= \varepsilon_p P + \varepsilon_{C_1} C_1 + \varepsilon_{C_2} C_2 + \varepsilon_R R - \frac{\mu_R R}{Y_R} \\
\frac{dR}{dt} &= \mu_R R - \varepsilon_R R \\
\frac{dN}{dt} &= k_R \frac{\mu_R R}{Y_R} + k_{C_1} \frac{\mu_{C_1} C_1}{Y_{C_1}} + k_{C_2} \frac{\mu_{C_2} C_2}{Y_{C_2}} - \frac{\mu_p P}{Y_p}
\end{aligned}$$

Fig. 4. Mathematical equations for populations and nutrient dynamics in the model ecosystem (see Figs. 1, 2).

biotic cycle (and also by plants during their growth). Nitrogen contained in detritus is extracted due to activity of reducers and made available again to the ecosystem.

The principal difference between our model ecosystem and previously advanced models of closed ecosystems is that in our model the growth of consumers is limited by the available energy in preys but not by the nitrogen conserved in preys (Alexeev, 1978; DeAngelis, 1992; Loreau, 1995; Cohen et al., 2000). Most of these previous estimates support the viewpoint that the growth of predators is constrained by energy but not by nutrient availability. Limitation of consumers by available energy enhances their importance in biotic cycles functioning because they allow a very rapid return of free nutrient to the environment whereas such return through mineralization of non-living matter is much slower process (see, for example, Odum, 1971). Due to this reason we cannot get rid of detritus and reducer chains by assuming the rate of decomposition to be high enough.

A system of differential equations that corresponds to the diagram (Figs. 1, 2) of the biotic cycle limited by nitrogen is, therefore, given in Fig. 4 where μ_p , ε_p , μ_{C_1} , ε_{C_1} , μ_{C_2} , ε_{C_2} , μ_R , ε_R are specific growth and death rates of producers, consumers of first and second order and reducers, respectively; Y_p , Y_{C_1} , Y_{C_2} , Y_R – yield coefficients for producer, consumers of first and second order and reducer populations, respectively. Specific growth rates are taken from a well known form suggested by Monod.

COMPUTER SIMULATIONS

It is believed that for small plankton animals such as infuzoria, daphnia and others energy consumption does not differ between laboratory and natural conditions. Based on literature data, we assume that the average generation time of daphnia at parthogenesis propagation is several (3-5) days with average birth number 10. The average specific growth rate of single cellular algae is 1-3 divisions per day. Yield of food consumption is 0.035 – 0.50. Concentration of algae in a range of 1.2 – 3.6 mg/l of dry weight provides saturated concentrations for the growth of predators (*Daphnia pulex*). For computer simulations we used a software package for system modeling Stella-II (High Performance System, inc., USA). The basic results of these simulation runs are described below.

CONCLUSIONS

1. At first we considered an increase in complexity of the biotic cycle starting from the simplest (*producer-detritus-reducer-nutrients*) and ending with the most complex (*producer-consumer of 1st order-consumer of 2nd order-detritus-reducer-nutrients*). We found that the flow of free energy obtained by the first trophic chain (measured by primary production) increases after introduction of the 1st order consumer and also by introduction of 2nd order consumer (Fig. 3). The influence of the second order consumer introduction (measured by the change of steady state primary production) was found to be less significant than introduction of the 1st order consumer into the simplest cycle.

2. Competition between two producers in a biotic cycle of any complexity always leads to an increase of primary production although a breakdown of the cycle is also possible (when new producer is less nutritional for the predator).

3. Competition between consumers of 1st order for the producer in the cycle (*producer-consumer 1 – detritus-reducer-nutrients*) results in an increase of primary production only if the new consumer is less effective in prey consumption than its predecessor. However, if the predator obtains a higher growth rate and higher yield, the flow of used energy may decrease after consumer introduction. Such features of consumer species are similar to the differences between *r* and *K*- selection species.

4. Based on these simulations of biotic cycle formation in a simple model ecosystem, we found a striking property: cooperative co-evolution of the cycle and its trophic chains that in most cases leads to an increase of the flow of energy fixed by the first chain (primary production).

REFERENCES

- Alexeev V.V., I.I. Krishev, M.S. Polyakova, and T.G. Sazikina, Dynamics and statistical mechanics of biogeocenosis with fixed mass of limiting biogenic element, in *Man and Biosphere*, 2, pp. 42-102, MSU Press, Moscow, 1978, (in Russian).
- Bril'kov, A.V., A.V. Babkin, E.A. Baranova, T.S. Chernyaeva, and N.S. Pechurkin, Simulation of biological evolution: opened microbial systems and model biocycles, in *Biospherics*, eds. G. Mesnard, A. Gorban, I. Karlin, pp. 7-56, AMSE Transactions, A, 14, AMSE Press, Tassin, France, 1994.
- Cohen Y., J. Pastor, and T. L. Vincent, Evolutionary strategies and nutrient cycling in ecosystem, *Evol. ecology research*, 2, 719-743, 2000.
- DeAngelis, D.L., *Dynamics of nutrient cycling and food webs*, Chapman & Hall, London, 1992.
- Gitelson, I.I., From biosphere to noosphere, *Life Support&Biosphere Science*, 6, 115-122, 1999.
- Jorgensen, S.E., B.C. Patten, and M. Straskraba, Ecosystems emerging:toward an ecology of complex systems in a complex future, *Ecol. Modelling*, 62, 1-28, 1992.
- Jorgensen, S.E., and J. Padiak, Does the intermediate disturbance hypothesis comply with thermodynamics?, *Hydrobiologia*, 323, 9-21, 1996.
- Loreau, M., Consumers as maximizers of matter and energy flow in ecosystems, *American Naturalist*, 145, 22-42, 1995.
- Morowitz, H.J., *Energy flow in biology, biological organization as a problem in thermal physics*, N.Y. e.al., 1968.
- Nicolis, G., and I. Prigogin, *Self-organization in nonequilibrium systems, from dissipative structures to order through fluctuations*, Wiley, New York, 1977.
- Odum, E.P., *Fundamentals of Ecology*, W.B. Saunders Comp., Philadelphia e. al., 1971.
- Odum, H.T., *Systems ecology*, Wiley, New York, 1983.
- Pechurkin, N.S., *Energetic aspects of over-organisms systems development*, Nauka, Novosibirsk, pp 1-113, 1982, (in Russian).
- Pechurkin, N.S., Biospherics: a new science, *Life Support&Biosphere Science*, 1, 85-88, 1994.
- Vernadsky, V.I., *Biosphere*, Leningrad, pp 1-146, 1926, (in Russian).

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